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Climate-driven changes to the spatio-temporal distribution of the parasitic nematode, *Haemonchus contortus,* in sheep in Europe.

Running head: Climate change and *Haemonchus contortus* in Europe

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Abstract

Recent climate change has resulted in changes to the phenology and distribution of invertebrates worldwide. Where invertebrates are associated with disease, climate variability and changes in climate may also affect the spatio-temporal dynamics of disease. Due to its significant impact on sheep production and welfare, the recent increase in diagnoses of ovine haemonchosis caused by the nematode *Haemonchus contortus* in some temperate regions is particularly concerning. This study is the first to evaluate the impact of climate change on *H. contortus* at a continental scale. A model of the basic reproductive quotient of macroparasites, Q_0, adapted to *H. contortus* and extended to incorporate environmental stochasticity and parasite behaviour, was used to simulate Pan-European spatio-temporal changes in *H. contortus* infection pressure under scenarios of climate change. Baseline Q_0 simulations, using historic climate observations, reflected the current distribution of *H. contortus* in Europe. In northern Europe, the distribution of *H. contortus* is currently limited by temperatures falling below the development threshold during the winter months and within-host arrested development is necessary for population persistence over winter. In southern Europe *H. contortus* infection pressure is limited during the summer months by increased temperature and decreased moisture. Compared with this baseline, Q_0 simulations driven by a climate model ensemble predicted an increase in *H. contortus* infection pressure by the 2080s. In northern Europe, a temporal range expansion was predicted as the mean period of transmission increased by 2-3 months. A bimodal seasonal pattern of infection pressure, similar to that currently observed in southern Europe, emerges in northern Europe due to increasing summer temperatures and decreasing moisture. The predicted patterns of change could alter the epidemiology of *H. contortus* in Europe, affect the future sustainability of contemporary

control strategies, and potentially drive local adaptation to climate change in parasite populations.

Introduction

Recent climate change has been associated with observable changes in the phenology and geographic distribution of invertebrates worldwide (Parmesan & Yohe, 2003; Root et al., 2003; Altizer et al., 2013; Kutz et al., 2013). Where invertebrates are associated with disease, climate variability and changes in climate may also affect the spatio-temporal dynamics of disease (Lafferty, 2009; Guis et al., 2011; Rose & Wall, 2011; Wall & Ellse, 2011; Altizer et al., 2013; Kreppel et al., 2014). Trichostrongyloid gastrointestinal nematodes (GINs) are particularly vulnerable to such changes as part of the life-cycle is completed outside the host (Anderson, 2000) and development, mortality and behaviour of the free-living stages is climate-dependent (O'Connor et al., 2006; Sutherland & Scott, 2010; Hernandez et al., 2013). The impact of predicted climate change on the distribution of *Haemonchus contortus*, a highly pathogenic, blood-feeding GIN infecting sheep and goats, is of particular concern due to the severity of haemonchosis, a form of parasitic gastroenteritis caused by *H. contortus* infection, which results in significant morbidity and mortality associated with blood loss.

Haemonchus contortus is typically associated with tropical and sub-tropical climates (O'Connor et al., 2006) and climatic limitations play a dominant role in characterising its spatial distribution (O'Connor et al., 2006; Bolajoko et al., 2015; Rinaldi et al., 2015). The impact of climate change on the spatio-temporal distribution of *H. contortus* is of particular interest in Europe, where heterogeneity in its spatial distribution has been attributed to regional variation in mean temperature and rainfall (Rinaldi et al., 2015). For example, temperatures fall below the minimum development threshold of ~9°C for at least part of the year in some northern (e.g. Sweden and the UK; Troell et al., 2005, Rose et al., 2015b) and alpine regions. In these regions, arrested development within the host is important for the survival over winter of populations of *H. contortus* (Waller et al., 2004), and limited

development and survival of the free-living stages during the cold season prevents infective stages accumulating on pasture, limiting infection pressure (Rose et al., 2015b). Consequently, potential increases in winter air temperature of over 5°C in northern Europe (IPCC, 2013) could result in an increase in the development and survival of *H. contortus* on pasture during winter, with subsequent increases in infection pressure and disease incidence. Development of larvae is also limited during periods of drought (Eysker et al., 2005), which are more common in southern Europe. Effects of excessively high temperatures and low rainfall in summer might therefore act to offset improved winter conditions for transmission and alter the seasonal epidemiology of haemonchosis, with implications for optimal management interventions.

Climate change impacts are likely to be greatest where *H. contortus* exists at the edge of its range of climatic tolerance (Lafferty, 2009) and changes in the spatial distribution and prevalence of haemonchosis have already been observed in the United Kingdom in recent decades. Van Dijk et al. (2008) identified an increasing trend in diagnoses of haemonchosis between 1989 and 2006, associated with an increase in temperatures over the same period. Furthermore, the emergence of ovine haemonchosis in Scotland in recent years has been associated with climate warming (Kenyon et al., 2009). Further epidemiologically significant changes in the seasonality of infection pressure (Rose et al., 2015b) and spatial distribution of *H. contortus* are therefore expected under scenarios of future climate change.

The impact of any changes on welfare, productivity and profitability could be wide-ranging if farmers are unable to respond effectively to these changes. Increased agricultural inputs (e.g. pharmaceutical products and additional feed) and decreased welfare associated with climate-driven increases in prevalence of haemonchosis or range expansion of *H. contortus* present a real threat to the future sustainability of the European sheep industry. Furthermore, the threat

of anthelmintic resistance (Rose et al., 2015a) presents a significant constraint to the adaptive capacity of farmers to changes in disease dynamics in the face of global change. There is therefore a need to develop sustainable animal health management strategies which optimise the use of available resources, underpinned by a detailed understanding of the potential impacts of global changes, including climate and environmental management, on parasites and disease dynamics. Empirical evidence can be used to make qualitative predictions of parasite responses to climate change (e.g. Altizer et al., 2013). However, the present study is the first to quantify the impact of climate change on *H. contortus* at a continental scale. To evaluate potential future climate-driven changes in the risk of haemonchosis in Europe, and interactions with livestock management, a model based on the basic reproductive quotient of macroparasites, Q_0 (Roberts & Heesterbeek, 1995), incorporating environmental stochasticity and sheep stocking density, was developed for *H. contortus* and applied at a Pan-European spatial scale.

Materials and methods

Q_0 Model description

The model was built on Roberts and Heesterbeek's (1995) basic reproduction quotient for macroparasites, Q_0, which provides a threshold quantity to predict the propensity of macroparasite populations to increase ($Q_0>1$) or decrease ($Q_0<1$) and therefore provides an index of infection pressure (Heesterbeek & Roberts, 1995; Roberts & Heesterbeek, 1995). Q_0 estimates the average number of second-generation mature adult worms produced by a single adult worm during its lifetime in the absence of density-dependent constraints such as immunity and within-host competition, (Heesterbeek & Roberts, 1995).

Roberts and Heesterbeek (1995) applied the Q_0 model (Equation 1) to the trichostrongylid nematode *Trichostrongylus colubriformis*, which, like *H. contortus,* follows a direct life cycle with in-host and free-living stages. Eggs are deposited on pasture in the faeces of the host where they hatch to produce larvae, which moult twice to reach the third, infective stage (L3). L3 then migrate horizontally out of the faeces when there is sufficient moisture and subsequently migrate between soil and herbage (vertical migration). L3 on herbage are accidentally ingested by the host during grazing, where upon they develop to the 4th larval stage (L4) and either undergo arrested development (hypobiosis) or continue to develop to the adult stage. Eggs produced by adult females are then passed in the sheep's (or goat's) faeces and the cycle continues. The Q_0 model can be interpreted as sub-components, which characterise two key processes in the trichostrongylid life-cycle: the number of L3 produced by an adult worm during its lifetime (A), based on fecundity (λ), adult mortality (μ) and the probability that an egg will develop to L3 (q); the number of adult parasites produced by each L3 (B), based on the establishment rate of ingested L3 (p), the mortality rate of L3 on pasture (ρ), ingestion rate

of L3 by the host (β) and the number of hosts (H) (Roberts and Heesterbeek 1995). Parameters are defined in Table 1.

$$Q_0 = \underbrace{\frac{q\lambda}{\mu}}_{A} \underbrace{\frac{\beta p}{\rho + \beta H} H}_{B} \quad (1)$$

The parameter q, describing the probability of an egg developing to L3 was expanded (Equation 2) as described by Bolajoko et al. (2015) to incorporate climate-dependence in the life-history of free-living stages, and an additional horizontal migration parameter (m_1). These changes allow for non-linear interactions between development (δ), survival (μ_i) and horizontal migration rates and address the importance of horizontal migration behaviour in determining the availability of L3 on pasture (Wang et al., 2014).

$$q = \frac{\delta m_1}{(\mu_e + \delta)(\mu_{l3} + m_1)} \quad (2)$$

A vertical migration parameter was added to the model in the present study, m_2, to reflect the distribution of infective third stage larvae (L3) between soil and herbage on pasture (Equation 3; Table 1).

$$Q_0 = \frac{q\lambda}{\mu} \frac{\beta p}{\rho + \beta H} H m_2 \quad (3)$$

The definition of Q_0 in the present study is therefore extended to include environmental stochasticity. Thus, Q_0 estimates, in the absence of density-dependent constraints and given current environmental conditions, the number of mature adult worms produced by a single

adult worm during its lifetime, and provides an instantaneous estimate of potential *H. contortus* infection pressure.

Model parameterisation

The proportion of total pasture L3 that are found on herbage, m_2, was set at a constant of 0.2 after van Dijk and Morgan (2011) recovered 20-30% of *H. contortus* L3 from herbage (corrected for recovery rate) and Callinan and Westcott (1986) recovered 4-23% of pasture L3 from herbage at temperatures between 10 and 30°C.

The functions for temperature-dependent development from egg to L3 (δ), and mortality of eggs (μ_e) and L3 (μ_{l3}) were derived from data in the literature as described previously (Rose et al., 2015b). Moisture rules constructed by Rose et al. (2015b) to estimate the effect of precipitation and evaporation on the development and migration of *H. contortus* were adapted to incorporate the combined effects of faecal moisture content on development and horizontal migration. Moisture availability in the 4 days preceding and following egg deposition is important for the development success and horizontal migration of *H. contortus* (O'Connor et al., 2008; Khadijah et al., 2013). Therefore a 9 day centred cumulative precipitation, *P*, and 9 day centred cumulative evaporation, *E*, was used to calculate *P/E* for each day. If $P/E<1$ then no eggs yielded L3 on pasture ($q=0$), whereas if $P/E\geq1$ then the probability of development to L3 and migration onto pasture (q) was estimated as a function of temperature (Table 1).

Temperature-dependent mortality rates of L3 on pasture, ρ, were estimated heuristically from the temperature-dependent mortality rates of L3 in faeces as described previously (Bolajoko et al., 2015).

Mean daily fecundity of adult female *H. contortus* was estimated to the nearest 100 from the results of individual experimental infections reported by Coyne and Smith (1992b). A 1:1 sex

ratio was assumed, therefore the mean fecundity per female worm was divided by 2 to estimate daily fecundity per adult worm, λ.

The instantaneous daily mortality rate of adult worms in the host, μ, was estimated from the mean proportion of unlabelled adult worms surviving 8 weeks in sheep infected with between 0 and 6000 radiolabelled L3 per week (Table 1 in Barger & LeJambre, 1988) as *–ln(mean proportion surviving)/56 days*. The mean proportion of unlabelled adults surviving 8 weeks was estimated by dividing the number of unlabelled adults recovered at necropsy on day 56 with the number of unlabelled adults recovered at necropsy on day 0.

The probability of establishment of *L3* following ingestion by the host, *p*, representative of immunologically naïve ovine hosts, was as reported by Barger et al. (Table 2 in Barger et al., 1985) for radiolabelled larvae administered to lambs that had been exposed to only 1 week of trickle infection with unlabelled larvae. Thus the labelled larvae that had established could be differentiated from the unlabelled larvae.

The rate at which larvae are ingested by host animals, β, was estimated as a function of herbage consumption rates, *c*, available biomass per unit area, *B*, and area of pasture, *A*, assuming that larvae are homogenously distributed on pasture (Table 1).

Current climate-driven variability in Q_0

To describe the current climate-driven spatio-temporal variability in Q_0 in Europe, the most up to date EOBS gridded climate dataset (0.25° x 0.25°) was used which is based on station measurements for Europe (Haylock et al., 2008). Rainfall (P) and mean (T_{mean}), minimum (T_{min}) and maximum (T_{max}) temperatures were available for the period 1950-2013 at daily temporal resolution. The model was applied to each cell in the gridded dataset and the resulting daily Q_0 estimates were aggregated to estimate annual decadal averages and monthly decadal averages for the 1970s (1970-1979), 1980s (1980-1989), 1990s (1990-1999) and 2000s (2000-2009).

Future climate-driven variability in Q_0

To assess the impact of likely future climate change on the spatial variability of Q_0 in Europe, a subset of five global climate models (HadGem2-ES; IPSL-CM5A-LR; MIROC-ESM-CHEM; GFDL-ESM2M; and NorESM1-M) produced within the Coupled Model Inter-Comparison Project 5 were used (Taylor et al., 2012). This subset was selected to give a wide range of predicted temperature and rainfall changes. As significant temperature and rainfall biases can be simulated by climate models with respect to climate observations, the simulated climatic variables were further calibrated by the Potsdam Institute for Climate Impact Research within the ISI-MIP project framework (Warszawski et al., 2014). This was carried out to ensure statistical agreement between the climate model outputs and the observed Watch Forcing Data dataset for 1960-1999 (Hempel et al., 2013). The Q_0 model was applied to three time windows (20 year averages): 2020s (2011 to 2030); 2050s (2041-2060) and 2080s (2071-2090). All climate model experiments were re-gridded to a uniform half degree square grid at global scale and are presented as ensemble means (mean predictions from all five global climate models) for the European domain [35.5ºN-71ºN, 12ºW-30ºE]. Data were available for four Representative Concentration Pathways (RCP) scenarios (RCP2.6, RCP4.5, RCP6.0, RCP8.5)

representing a range of radiative forcings, from the mildest (RCP2.6) to the most extreme (RCP8.5) emissions scenario (Moss et al., 2010).

Finally, to assess the overall impact of likely future climate change on seasonal variation in Q_0 in Europe, mean monthly current and future Q_0 estimates were calculated from the daily gridded estimates for the baseline period (1971-2010) using both EOBS data and the equivalent control (CTL) CMIP5 dataset, and for the 2080s under the RCP2.6 and RCP8.5 scenarios, for Northern Europe [48°N-59°N, 12°W-18.5°E] and Southern Europe [35.5°N-44°N, 10°W-18.5°E].

Climate-management interactions

The impact of climate-management interactions on Q_0 predictions was explored by comparing estimates using the current climatic data and either a regionally variable sheep stocking density or a uniform host density of 1. All future Q_0 estimates used the regionally variable sheep stocking density values. For this, a gridded dataset (0.25° x 0.25°) of livestock units (LSU) per hectare of pasture were derived from an aggregated NUTS 3 (Nomenclature Units for Territorial Statistics; EUROSTAT) regional sheep stocking density dataset (Fig. S1; Phelan et al., 2014). Data were presented in LSU per hectare and multiplied by 10 to obtain sheep per hectare (European Commission, 2009).

Results

In the absence of moisture limitations, Q_0 peaked at 20°C, decreasing at higher and lower temperatures due to a trade-off between development and mortality rates (Fig. 1). Q_0 was zero below the predicted lower threshold for development of 9.16°C.

Current climate-driven variability in Q_0 and climate-management interactions

There was considerable spatial variability in the annual mean decadal Q_0 predictions (Fig. 2) associated with climate variability. $Q_0>1$ (i.e. an increasing population) was predicted throughout Europe whereas $Q_0<1$ (i.e. decreasing population) was restricted to a few scattered locations in Northern Italy, Eastern Poland, Norway, Bulgaria and the Austria-Slovakia border. Comparison of Q_0 estimates using spatially variable and constant sheep stocking density (H=1) (Fig. 3) indicates that Q_0 is moderated by climate-management interactions whereby Q_0 is increased by higher sheep stocking density (e.g. Norway) and decreased by low sheep stocking density (e.g. eastern Poland).

There was also significant seasonal variability in Q_0 predictions across Europe. Throughout much of Europe, Q_0 values below the critical threshold ($Q_0=1$) were simulated during the winter months (December – February), indicating suppressed transmission and population decline (Figs. 4 & 5). In Norway, Sweden and Finland this period extended to October-May. Thus, between 1970 and 2013 $Q_0<1$ was predicted in these regions for 8 months of the year (Fig. 4). $Q_0>1$ (an increasing population) was predicted for much of Europe between April and November as temperatures rose above the threshold for development (Figs. 4 & 5). However, in some Southern European regions such as Portugal and Spain, the opposite seasonal dynamic was predicted as temperatures remained sufficiently high over winter to allow the development

and survival of *H. contortus*, but conditions were unfavourable for *H. contortus* during the summer months due to increasing temperatures and decreased rainfall. As a result, $Q_0<1$ (population decline) was predicted between June and August in some areas in southern Europe and mean Q_0 for the region was low (Figs. 4 & 5b). Monthly decadal output using a variable and constant sheep stocking density is provided as supplementary information (Figs. S2-S9).

Future climate-driven variability and patterns of change in predicted Q_0

A general increase in future Q_0 was predicted (Figs. 5 & 6), driving annual Q_0 above the critical threshold throughout the majority of Europe under all RCPs and all time periods tested (Fig. 7). A greater change was predicted in northern Europe than in southern Europe (Figs. 5 & 6). There are large uncertainties in the multi-model projections. These uncertainties generally increase as a function of time and as a function of severity of emissions (Fig. 5).

The increase in mean annual Q_0 estimates can be attributed to predicted increases year-round in northern Europe (Fig. 5a) and during the autumn and winter months in southern Europe (Fig. 5b). In addition, due to predicted increases in temperatures and moisture limitations during the summer months under the RCP8.5 scenario, a decrease in Q_0 was simulated in northern Europe prior to the peak in September-October (Fig. 5a). This aligns more closely with the current bimodal seasonal pattern of Q_0 in southern European regions, albeit with a significantly greater predicted Q_0 than in current climate.

Discussion

The impact of climate change on the spatio-temporal distribution of the haematophagous nematode, *H. contortus*, was investigated using an environmentally stochastic model of the basic reproductive quotient (Q_0), which provides estimates of potential infection pressure given prevailing environmental conditions and a threshold quantity to estimate population persistence. Using baseline climatic data representative of the period 1971-2010, $Q_0<1$ was predicted for northern Europe between November and March as low temperatures limit the development and survival of the free-living stages during the winter period. This reflects observations in these regions that *H. contortus* is dependent on the arrested development of fourth stage larvae in the host (hypobiosis; Waller et al., 2004; Sargison et al., 2007) and to a lesser extent L3 sequestered in soil (Rose et al., 2015b) to survive the winter period. Simulations using both the RCP2.6 and RCP8.5 climate change scenarios predicted a mean increase in the future transmission season of 2-3 months such that mean Q_0 is greater than 1 throughout the year in northern Europe. This predicted future increase in infection pressure in northern Europe may result in an increased incidence of haemonchosis if current control strategies are insufficient and farmers fail to adapt. Furthermore, simulations of *H. contortus* population dynamics suggest that the extended period where temperatures remain above the threshold for development may magnify the predicted increase in infection pressure as a result of an increase in cumulative pasture contamination, and a decrease in total L3 mortality during periods that are unfavourable for development (Rose et al., 2015b). The predicted shift in the geographical range of the free-living stages of *H. contortus* during the winter months may relinquish *H. contortus* of the selection pressures driving winter hypobiosis (Gaba & Gourbière, 2008), presenting a target for local adaptation to climate change, and increasing infection pressure during this period.

In addition to the predicted increase in infection pressure during the winter months in northern Europe, a decrease in infection pressure during the late summer months was predicted due to an interaction between increased temperature-dependent mortality and development rates, and moisture limitations on development success and migration onto pasture (*q*). This was more pronounced under RCP8.5 than RCP2.6. The emergence of a bimodal pattern of seasonal infection pressure appears to be a consistent prediction for GINs in temperate and Arctic regions under various scenarios of climate change; a similar pattern was predicted for the GINs *H. contortus, Teladorsagia circumcincta* and *Ostertagia ostertagi* infecting ruminants in England (Rose et al., 2015b), and *O. gruehneri* infecting caribou in North America (Molnár et al., 2013), as well as other parasitic helminths in northern Europe (*Fasciola hepatica;* Caminade et al., 2015) and invertebrate ectoparasites in Great Britain (*Lucilia sericata;* Rose & Wall, 2011; Wall & Ellse, 2011). This "summer dip" in infection pressure may play a role in moderating the impact of climate change in northern Europe (Rose et al., 2015b).

The predicted future bimodal pattern of infection pressure predicted for *H. contortus* in northern Europe is currently observed in southern Europe where, on average, winter temperatures are high enough to permit development and survival of the free-living stages, yet moisture limitations and high temperatures during the summer months limit development success. Q_0 is predicted to increase in southern Europe during the winter months under RCP8.5, while a longer summer break in transmission is predicted where Q_0 falls below 1. In contrast to the decrease in selection pressure for winter hypobiosis in northern Europe, hypobiosis may become increasingly important as a strategy for the future summer survival of *H. contortus* in southern Europe due to the predicted future reduction in Q_0 during the hot, dry summer months increasing the selection pressure for summer hypobiosis. Similar patterns

134 are seen in semi-arid regions such as Kenya, where hypobiosis is an important strategy for the
135 survival of *H. contortus* during the dry periods when the transmission of free-living stages is
136 limited (Gatongi et al., 1998).

137 In addition to climate variability other environmental and livestock management factors that
138 may affect disease risk vary from region to region within Europe due to differing socio-
139 economic, policy and bioclimatic drivers e.g. land use and stocking rates. The contribution of
140 livestock management to spatial variability in disease risk may even outweigh the
141 contribution of climate and provide an opportunity to mitigate the impact of climate change
142 (Morgan & Wall, 2009). By considering the interacting effects of host (sheep) stocking
143 density and climate on Q_0 insights have been gained into the drivers of spatial variability in
144 disease risk. Sheep stocking density moderated the effect of climate variability, increasing
145 spatial heterogeneity in Q_0 predictions. For the majority of Europe, a higher Q_0 was predicted
146 under current regional sheep stocking densities compared with a constant sheep stocking
147 density (1 sheep ha^{-1}), suggesting that current European sheep stocking densities enhance
148 infection pressure and transmission risk of *H. contortus*. Therefore, predicted future increases
149 in infection will be exacerbated in regions where high future stocking densities are necessary
150 due to limitations such as land availability. However, the extent to which environment and
151 livestock management are likely to change in response to climate change and altered patterns
152 of parasite transmission is difficult to estimate, particularly where host immunity,
153 farm/environmental management, climate and parasites interact (Rohr et al., 2011), and
154 where economic considerations are of paramount importance. Furthermore, the behaviour of
155 farm managers may lag behind the optimal response to climate-driven changes, for example
156 due to variability in adaptive capacity and perception of resilience and risk (Marshall, 2010).
157 As a result, it is common, as in this study, to make climate change impact assessments under

158 the assumption of no change in management. Some recent progress has been made in
159 estimating the impact of climate change on management factors relevant to the epidemiology
160 of gastrointestinal helminths such as *H. contortus*, such as grazing season length (Phelan et
161 al., 2015). However, this remains a knowledge gap that can largely only be addressed by
162 evaluation of comparative management scenarios (Morgan & Wall, 2009; Wall & Ellse,
163 2011).

164 A previous adaptation of the Q_0 model to *H. contortus* was successful in replicating broad-
165 scale regional variation in frequency of *H. contortus* in the gastrointestinal nematode fauna of
166 sheep (Bolajoko et al., 2015). Using daily climatic data and with the addition of a vertical
167 migration parameter and variable sheep stocking density, the Q_0 model presented here
168 replicates qualitative spatio-temporal patterns of infection pressure, intensity of infection and
169 incidence of haemonchosis in Europe. The predicted optimal conditions for Q_0 were similar to
170 those previously observed experimentally *in vitro* (Coyne & Smith, 1992a) and *in vivo* (Rose,
171 1963). In the UK, peak diagnoses of haemonchosis are generally made between July and
172 October (van Dijk et al., 2008) corresponding with the peak Q_0 predictions for the region. In
173 Sweden, the absence of infection by *H. contortus* in naive lambs turned out onto pasture in
174 May (tracer lambs) indicates minimal overwinter survival of *H. contortus* on pasture in the
175 region (Waller et al., 2004) and reflects the extended period where $Q_0<1$ was predicted for the
176 majority of Sweden in the current study. The predicted decrease in summer Q_0 in southern and
177 Mediterranean regions is reflected in previously observed decreases in the recovery of *H.*
178 *contortus* infective stages from pasture samples in North Limousin, France, during the summer
179 months (Gruner et al., 1980) and reduced intensity of *H. contortus* infection during the summer
180 in naturally infected goats in Central Spain compared with spring and autumn (Valcárcel &
181 Romerro, 1999).

Potential limitations of the Q_0 approach adopted here lie primarily in the instantaneous nature of the model. For example, the cumulative impact of changes in development and survival of free-living stages on seasonal and inter-annual variation in infection pressure are not captured by the Q_0 model. Furthermore, the development of immunity and the annual rise in faecal egg counts in ewes around the time of parturition (periparturient rise) due to the relaxation of immunity and subsequent resumption of development of larvae that have overwintered as hypobiotic larvae in the host is not included in the model. Therefore changes in the magnitude of the periparturient rise as a result of changes in infection pressure in the previous grazing season are not predicted. However, additional complexity is required to incorporate host-parasite interactions in sufficient detail to capture these processes e.g. Learmount et al. (2006). The simplicity of the Q_0 models thus provides a tractable solution to predicting patterns of change in infection pressure and disease risk in response to changing climate and management at broad spatial and temporal scales. This is especially appropriate for *H. contortus*, in which egg shedding rates are often high and transmission success depends largely on climatic conditions over a short period of time. General predictions of likely changes in seasonal patterns of transmission potential, such as presented here, are likely to usefully inform parasite control strategies even without additional biological and management detail e.g. by identifying regions where climate change is predicted to have the greatest impact (Rohr et al., 2011).

In conclusion, an overall increase in infection pressure is predicted for *H. contortus* in Europe under a range of climate change scenarios. Predicted increases and changes in seasonal patterns of infection pressure were greater in northern Europe than in southern Europe, supporting the hypothesis that climate change impacts will be greatest where species exist at the edge of their range (Lafferty, 2009; Rohr et al., 2011), and suggesting that sheep and goat

producers in northern Europe are likely to be hardest hit by climate change impacts on *H. contortus*. Failure to adapt management to these changes could significantly impact animal welfare and threaten the future sustainability of the livestock industry in affected regions.

Competing interests

We have no competing interests

Authors' contributions

HR extended the Q_0 model and defined model parameters, participated in the design of the study and prepared the manuscript; CC acquired and prepared climatic data, carried out model integrations, participated in the design of the study and prepared the manuscript; MBB contributed to the development of the climate-dependent model components; PP acquired and prepared livestock stocking density data and participated in the design of the study; JvD designed and coordinated the study; MB and DW participated in the study design; ERM conceived, designed and coordinated the study. All authors contributed to early drafts of the manuscript and gave final approval for publication.

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Fig. 1. Temperature-dependent *H. contortus* Q_0 parameters in the absence of moisture limitations and with sheep stocking density (H) equal to 1. Parameters are defined in Table 1.

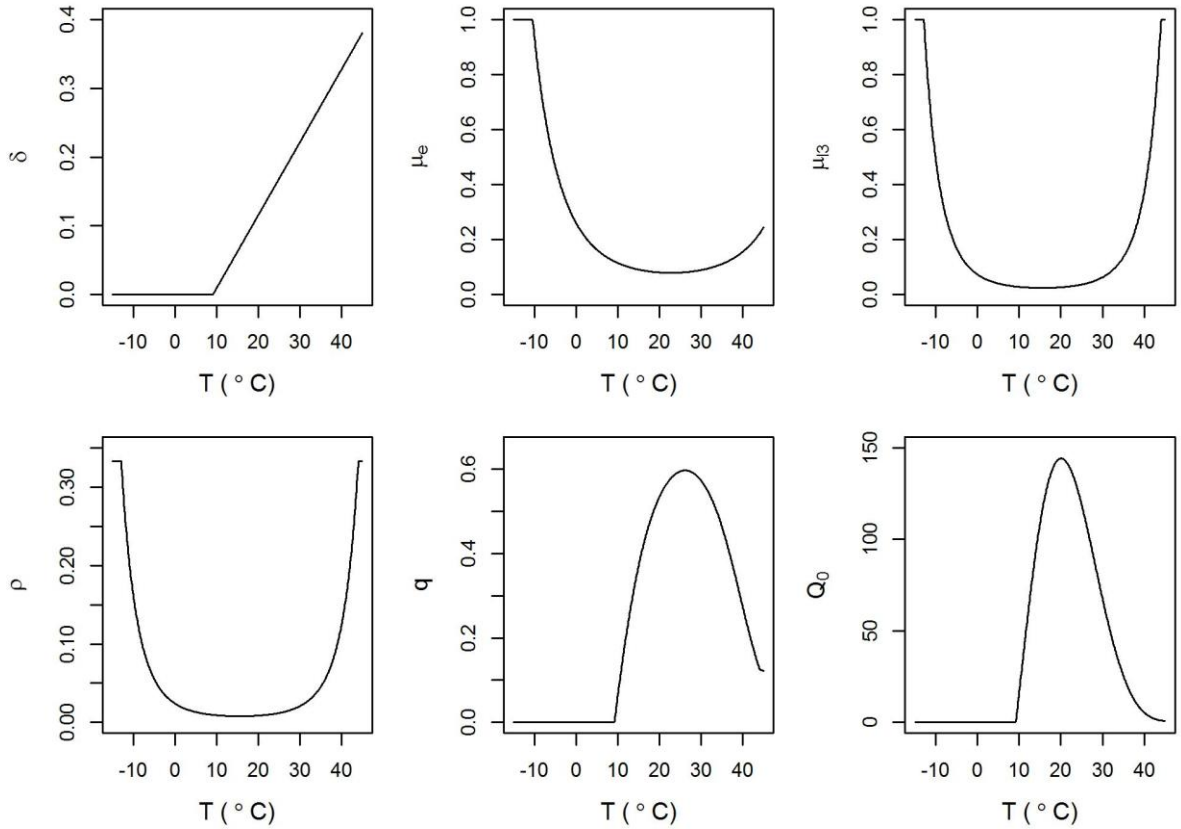
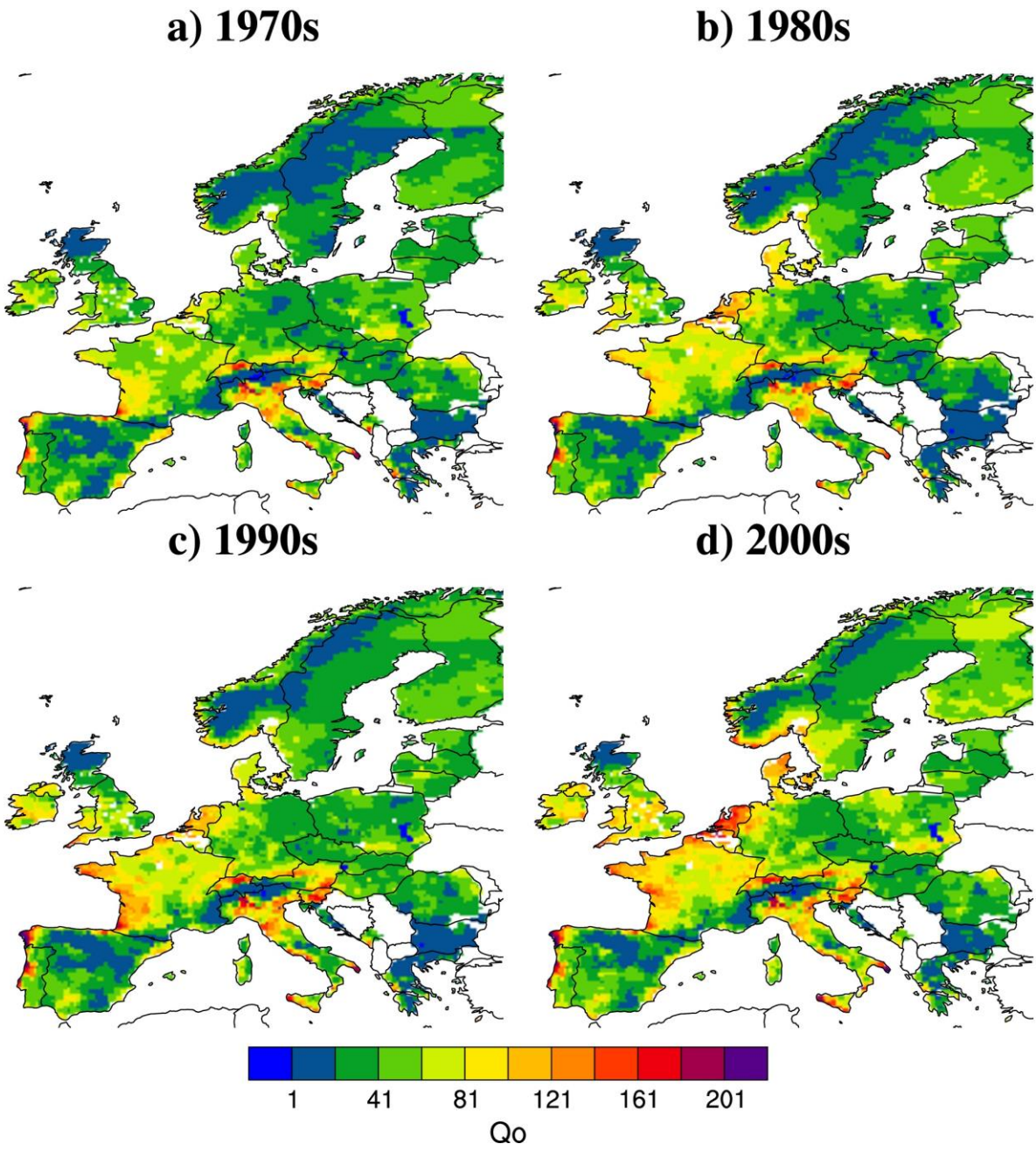


Fig. 2. Annual Q_0 estimates for (a) the 1970s, (b) the 1980s, (c) the 1990s and (d) the 2000s using the EOBS climate dataset and regionally variable sheep stocking density (Fig. S1; Phelan *et al.*, 2014). The white shading depicts regions for which no sheep stocking density data were available.



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429 **Fig. 3.** Annual Q_0 estimates for (a) the 1970s, (b) the 1980s, (c) the 1990s and (d) the 2000s

430 using the EOBS climate dataset. Q0_HCT indicates that these simulations used a constant

431 sheep stocking density (H=1). Note the difference in scale of Q_0 compared with Fig. 2.

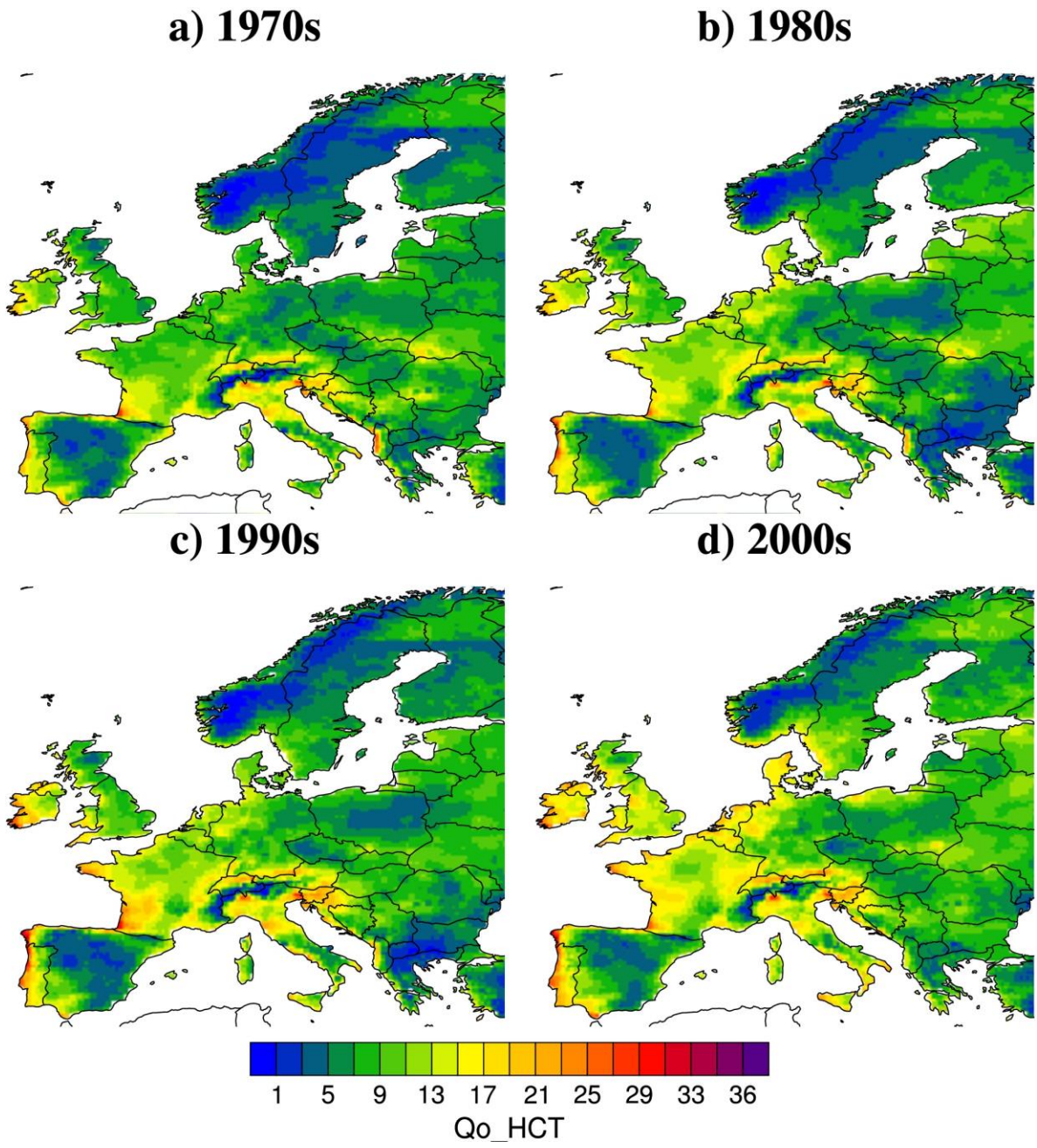

Fig. 4. Monthly Q_0 estimates based on the EOBS climate data for 1970-2013 and a spatially variable sheep stocking density (Fig. S1; Phelan et al., 2015). The white shading depicts regions for which no sheep stocking density data were available.

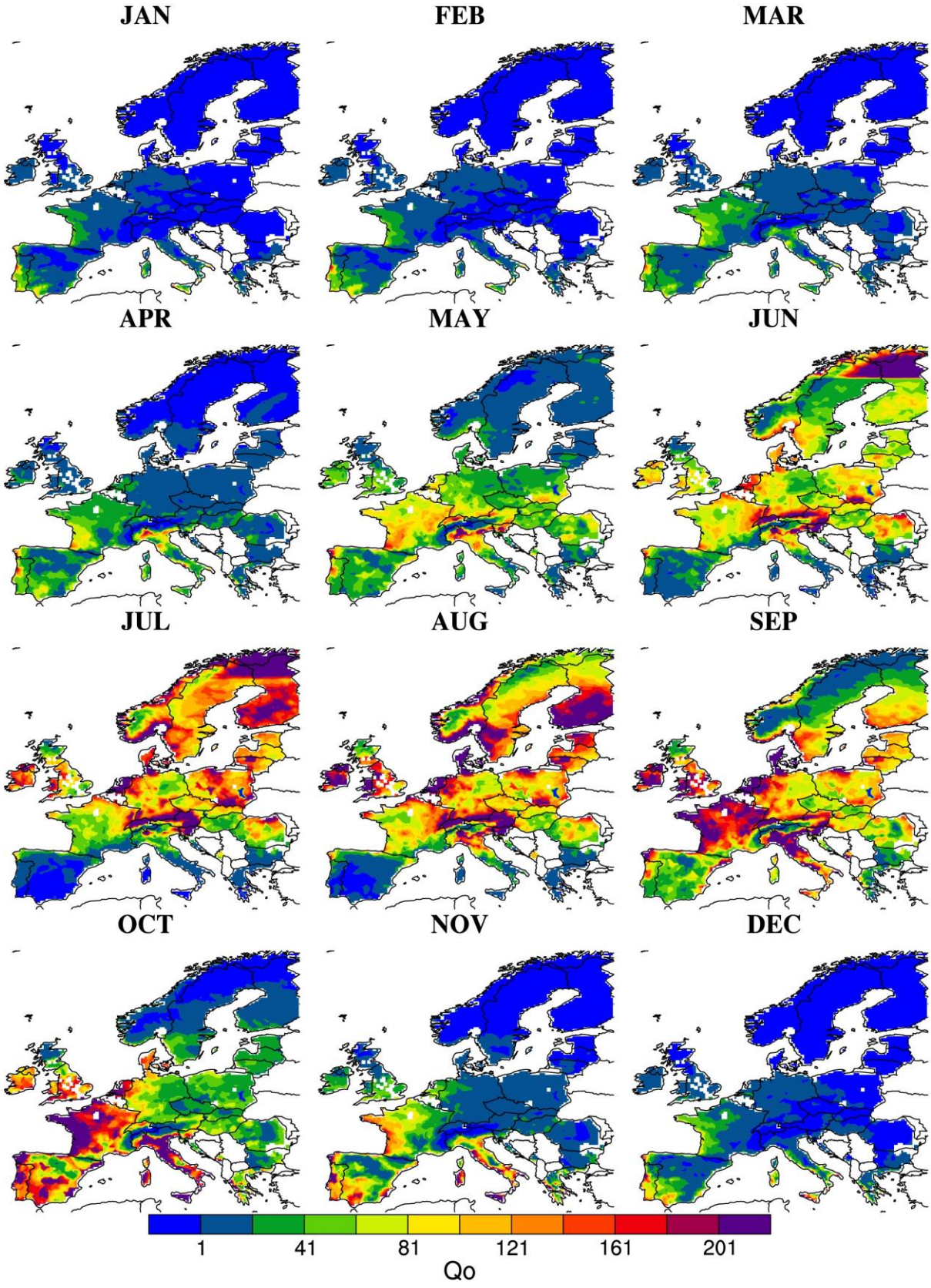
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Fig. 5. Change in Q_0 seasonality for (a) Northern Europe [48ºN-59ºN, 12ºW-18.5ºE] and (b) Southern Europe [35.5ºN-44ºN, 10ºW-18.5ºE]. The solid black line shows the Q0 model driven by the EOBS climate observations (1971-2010 average). The solid blue lines show the Q0 model driven by the ensemble mean over the same time period. The solid orange and red lines respectively show the ensemble mean of the Q0 simulations driven by the climate model ensemble for 2071-2090 under the RCP2.6 and RCP8.5 emission scenarios. Dotted lines depict the minimum and maximum within the model ensemble to assess the relative uncertainties.

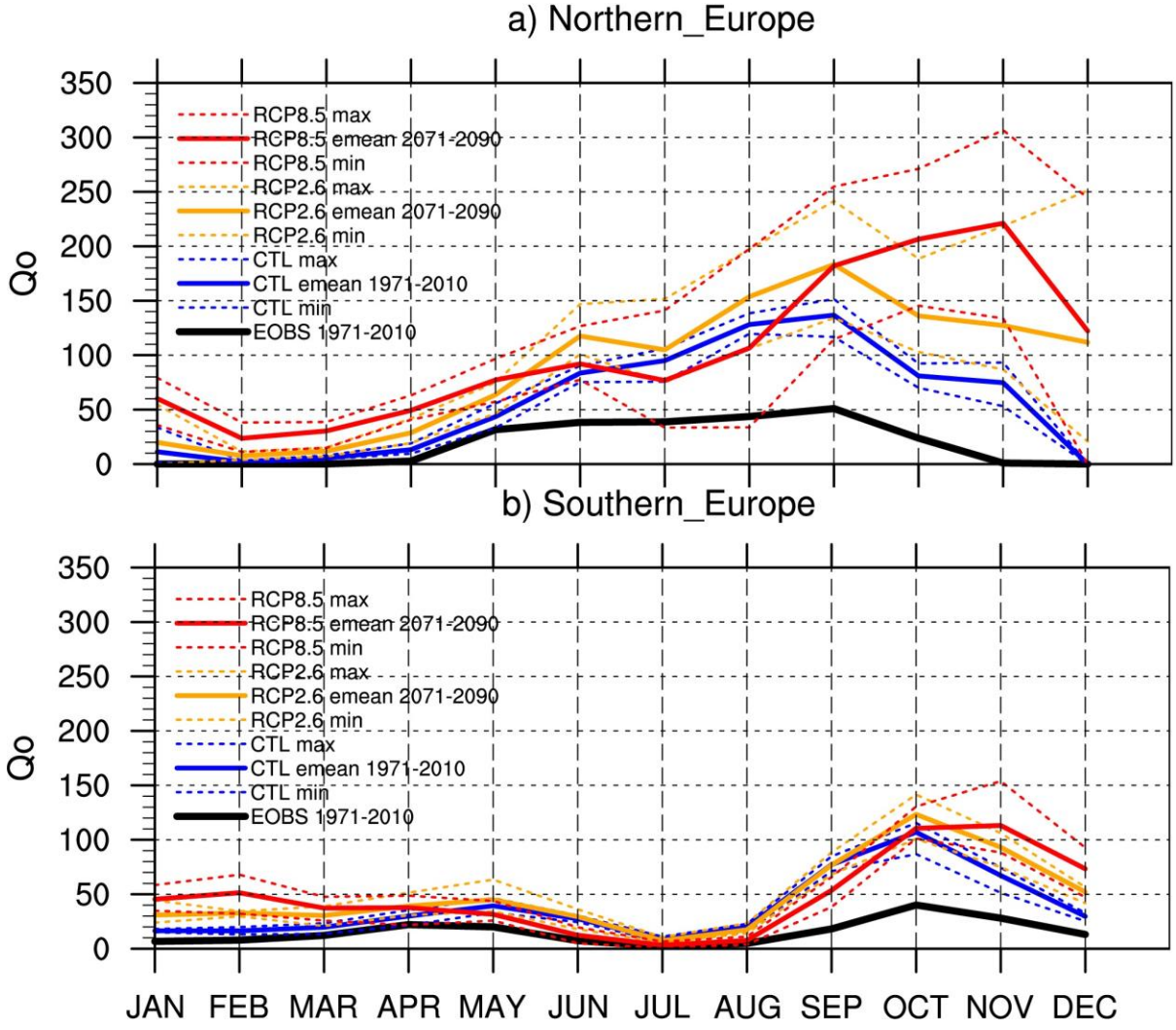


Fig. 6. Change in annual mean Q_0 based on the ensemble mean (Emean) of five climate models shown as future predicted Q_0 anomalies. Q_0 was estimated using the five global climate models for different time slices (rows) and different emission scenarios (columns, lowest e.g. RCP2.6 to highest RCP8.5 emission scenario from left to right). Anomalies have been calculated with respect to the historical experiments (1951-2005 baseline). The white shading depicts regions for which no sheep stocking density data were available.

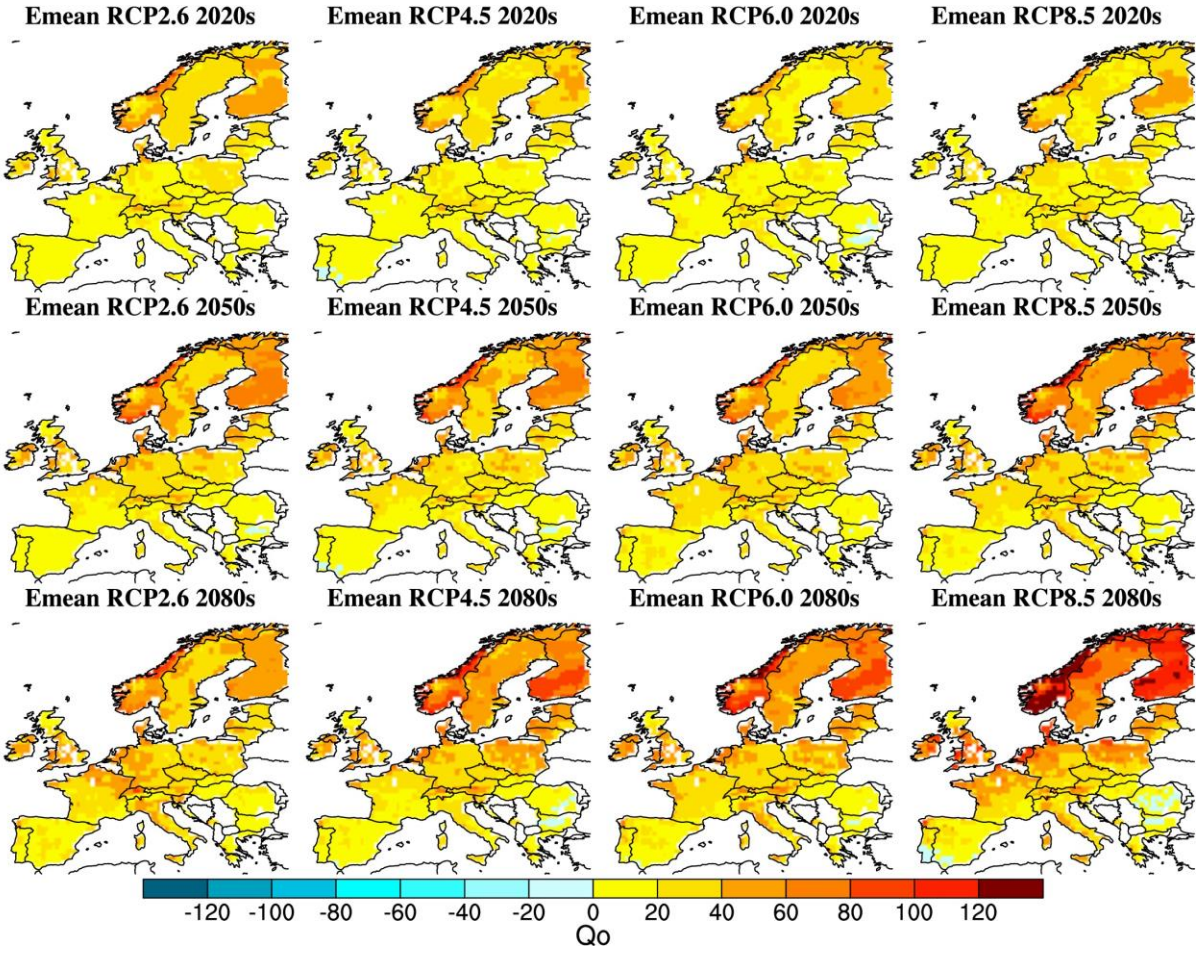
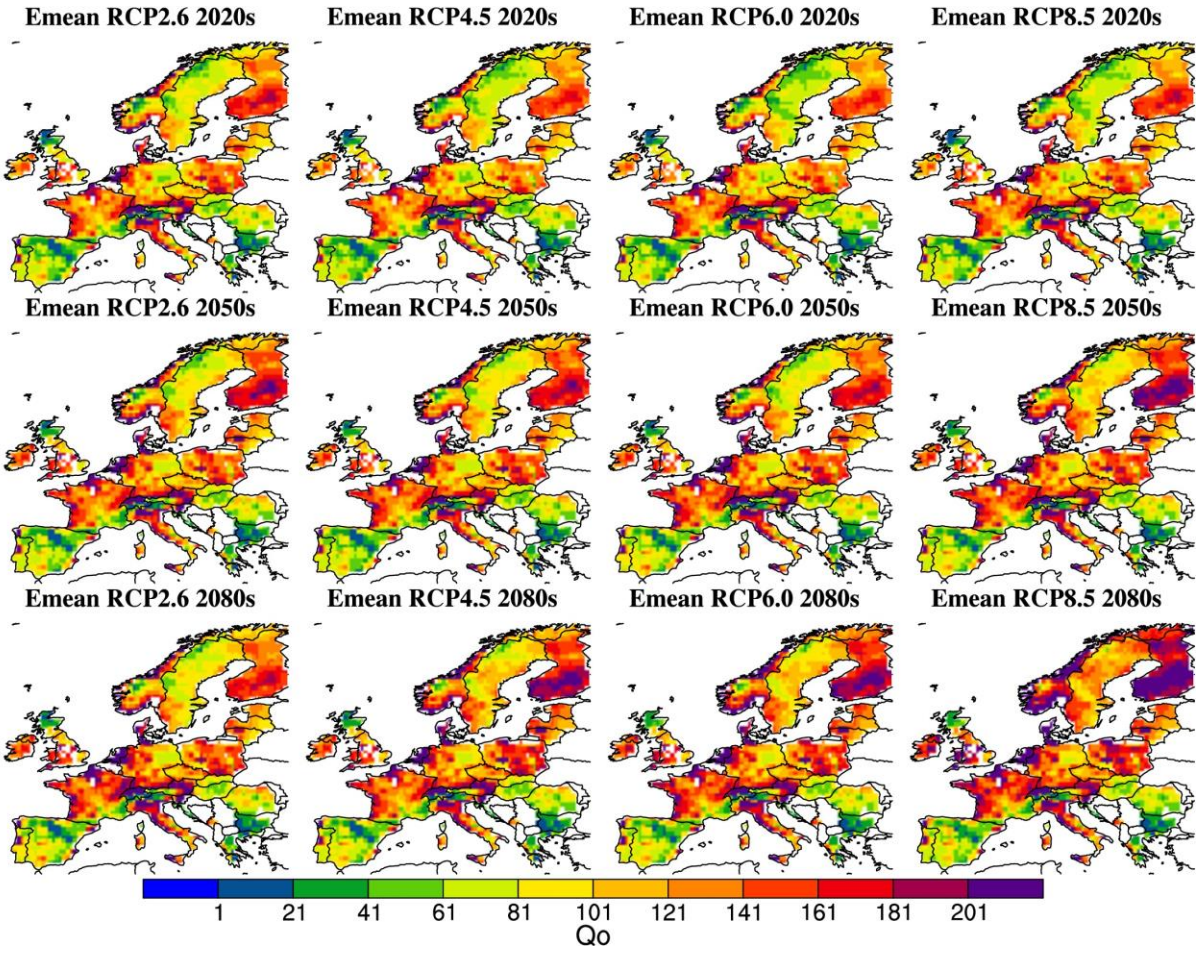


Fig. 7. Absolute annual mean Q_0 values based on the ensemble mean (Emean) of five climate models. Q_0 was estimated using the five global climate models for different time slices (rows) and different emission scenarios (columns, lowest e.g. RCP2.6 to highest RCP8.5 emission scenario from left to right). The white shading depicts regions for which no sheep stocking density data were available.


Emean RCP2.6 2020s
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461 **Table 1.** Extended Q_0 model parameter definitions and estimates.

Parameter	*Definition*	*Value*	*Source*
H. contortus			
λ	Fecundity (eggs day^{-1} adult^{-1})	2250	Coyne & Smith, 1992b
μ	Instantaneous daily mortality rate of adult nematodes	0.05	Barger & LeJambre, 1988
q	Probability that an egg will develop to L3 and migrate onto pasture	$\begin{cases} \frac{\delta m_1}{(\mu_e+\delta)(\mu_{l3}+m_1)}, & P/E \geq 1 \\ 0, & P/E < 1 \end{cases}$	O'Connor et al., 2008; Khadijah et al., 2013; Rose et al., 2015b
δ	Instantaneous daily development rate of eggs to L3	$-0.09746 + 0.01063T_{mean}$	Rose et al., 2015b

μ_e	Instantaneous daily mortality rate of eggs	$exp(-1.3484 - 0.10488T\ + 0.00230{T_{mean}}^2)$	Rose et al., 2015b
μ_{l3}	Instantaneous daily mortality rate of L3 in faeces	$\exp(-2.62088 - 0.14399T + 0.00462{T_{mean}}^2)$	Rose et al., 2015b
m_1	Instantaneous daily L3 migration rate between faeces and pasture	0.25	Rose et al., 2015b
ρ	Instantaneous daily mortality rate of L3 on pasture	$\mu_{l3}/3$	Bolajoko et al., 2015
m_2	Proportion of total pasture L3 that are found on herbage	0.2	Callinan & Westcott, 1986; van Dijk & Morgan, 2011
p	Probability of establishment of ingested L3	0.4	Barger et al., 1985

Host management			
β	Rate of ingestion of L3 on pasture	$\frac{c}{BA}$	-
c	Daily herbage dry matter intake per host (kg DM day^{-1})	1.4	Kao et al., 2000
H	Host density or stocking density (sheep ha^{-1})	Either regionally variable or held constant	Phelan et al., 2014
B	Standing biomass (kg DM ha^{-1})	2000	Leathwick et al., 1992; Kao et al., 2000
A	Grazing area (ha)	1	-
Climate			

P	Total daily precipitation (mm)		Daily variable	Haylock et al., 2008; Taylor et al., 2012
E	Daily potential evapotranspiration (mm day^{-1})	$0.0023 \times 0.408 \times Ra\left(\frac{T_{max}+T_{min}}{2}+17.8\right)\sqrt{T_{max}-T_{min}}$		Hargreaves & Samani, 1985
Ra	Extra-terrestrial radiation (MJm^{-2}day^{-1})		Daily variable	Anon, 2002
T_{mean}	Mean daily temperature (°C)		Daily variable	Haylock et al., 2008; Taylor et al., 2012
T_{min}	Minimum daily temperature (°C)		Daily variable	Haylock et al., 2008; Taylor et al., 2012
T_{max}	Maximum daily temperature (°C)		Daily variable	Haylock et al., 2008; Taylor et al., 2012

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SUPPORTING INFORMATION

Fig. S1. Livestock units (LSU) per hectare derived from Phelan et al. [32]. 1 LSU = 10 sheep.

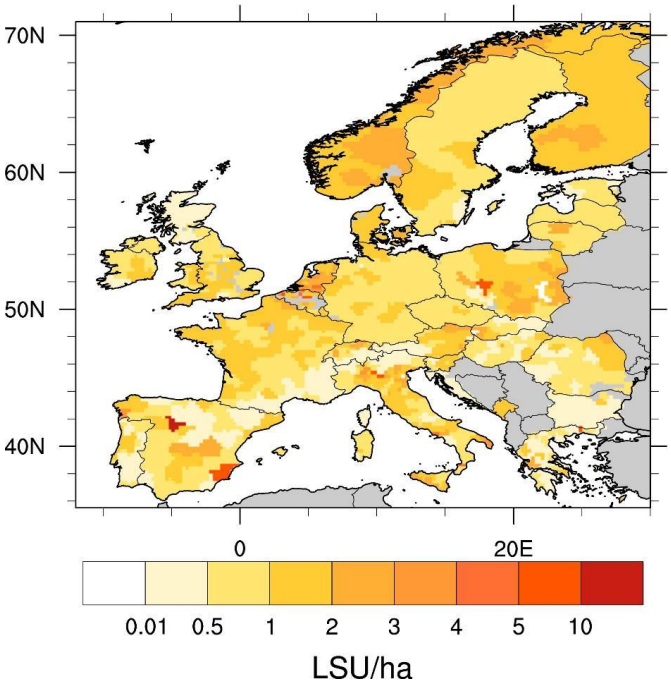

Fig. S2. Monthly Q_0 estimates based on the EOBS climate data for the 1970s (1970-1979) and a spatially variable sheep stocking density (Fig. S1; *Phelan et al.*, 2014). The white shading depicts regions for which no sheep stocking density data were available.

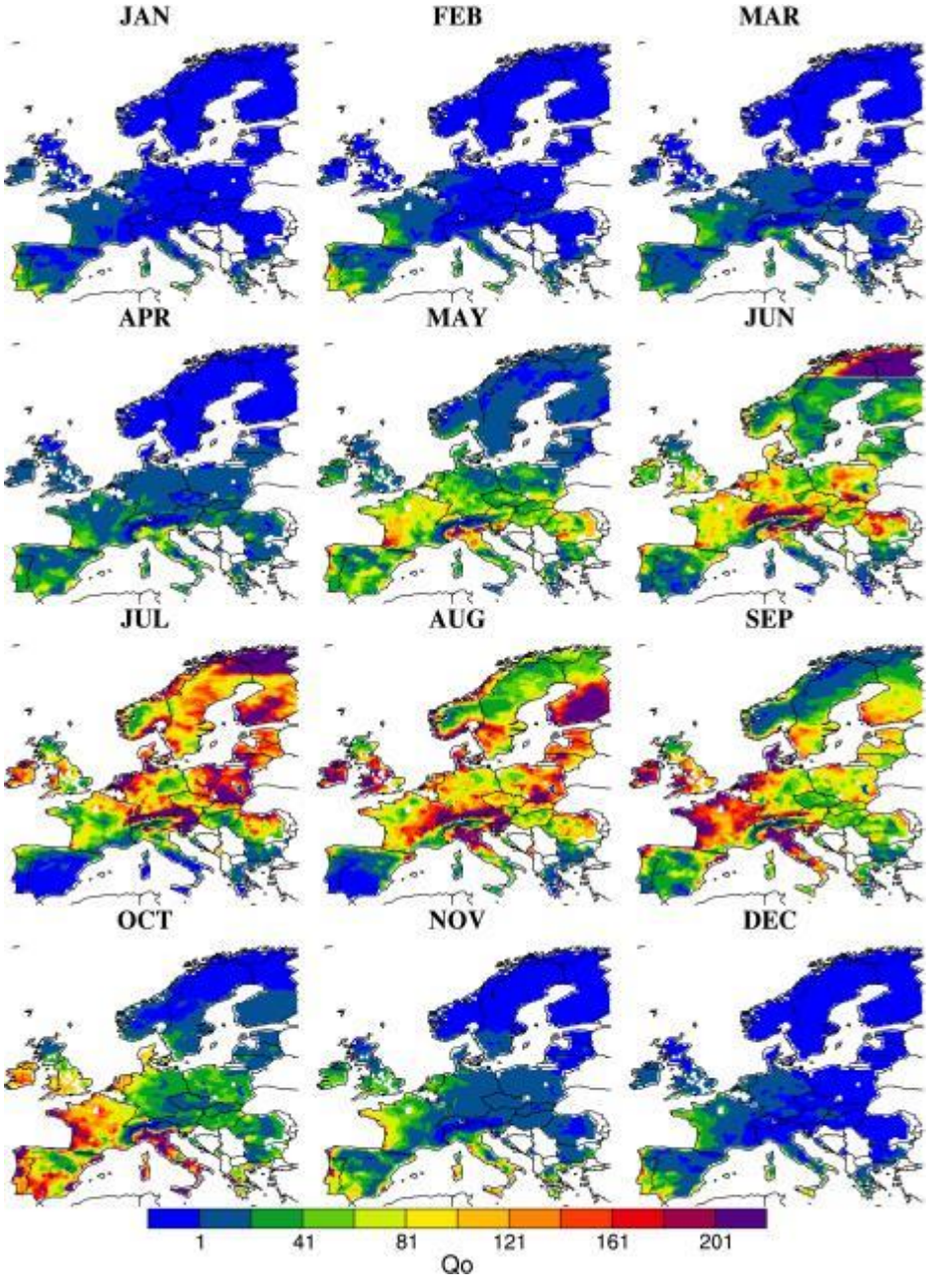

Fig. S2. Monthly Q_0 estimates based on the EOBS climate data for the 1980s (1980-1989) and a spatially variable sheep stocking density (Fig. S1; Phelan *et al.*, 2014). The white shading depicts regions for which no stocking density data were available.

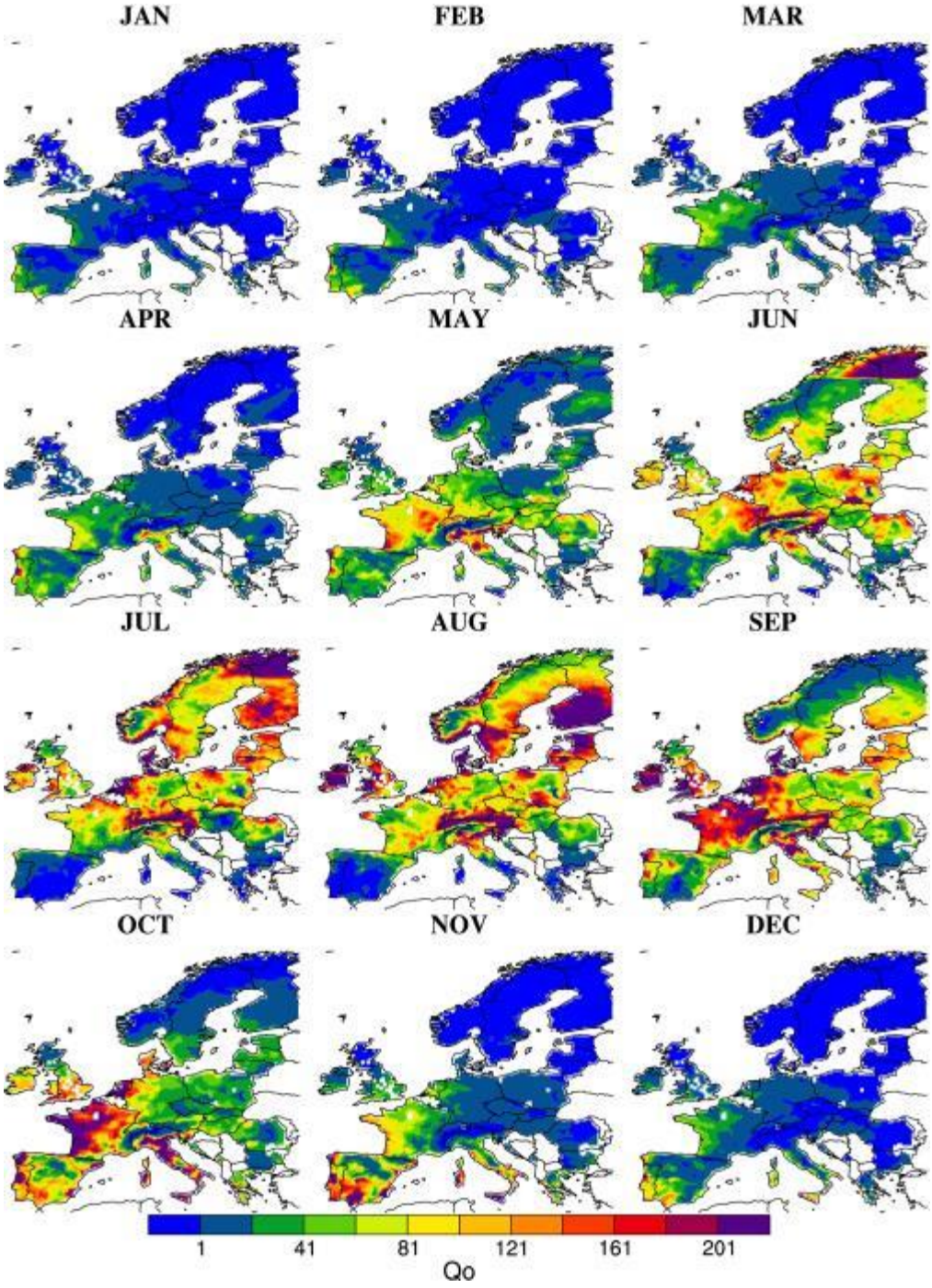

Fig. S3. Monthly Q_0 estimates based on the EOBS climate data for the 1990s (1990-1999) and a spatially variable sheep stocking density (Fig. S1; Phelan *et al.*, 2014). The white shading depicts regions for which no stocking density data were available.

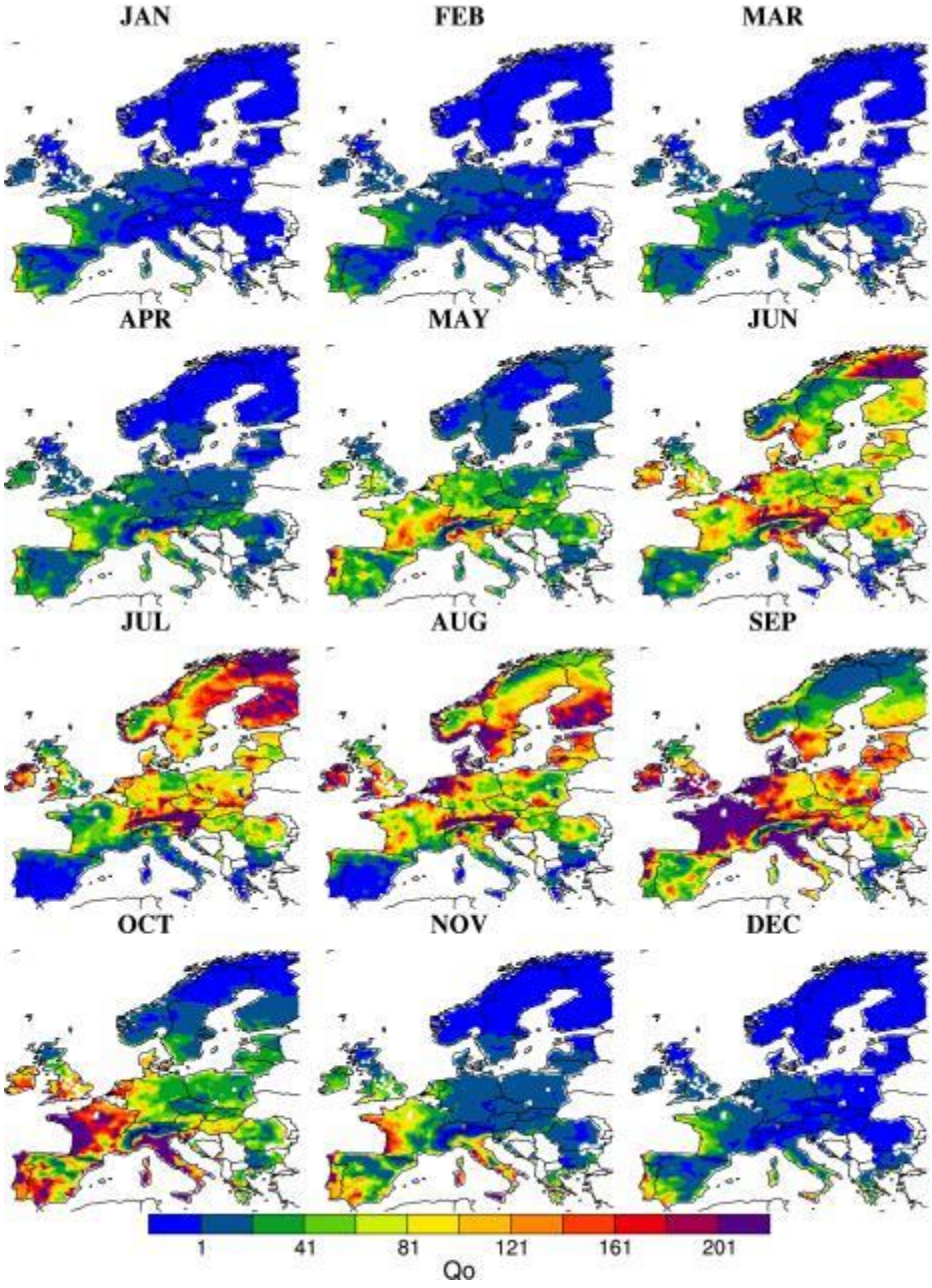

Fig. S4. Monthly Q_0 estimates based on the EOBS climate data for the 2000s (2000-2009) and a spatially variable sheep stocking density (Fig. S1; Phelan *et al.*, 2014). The white shading depicts regions for which no stocking density data were available.

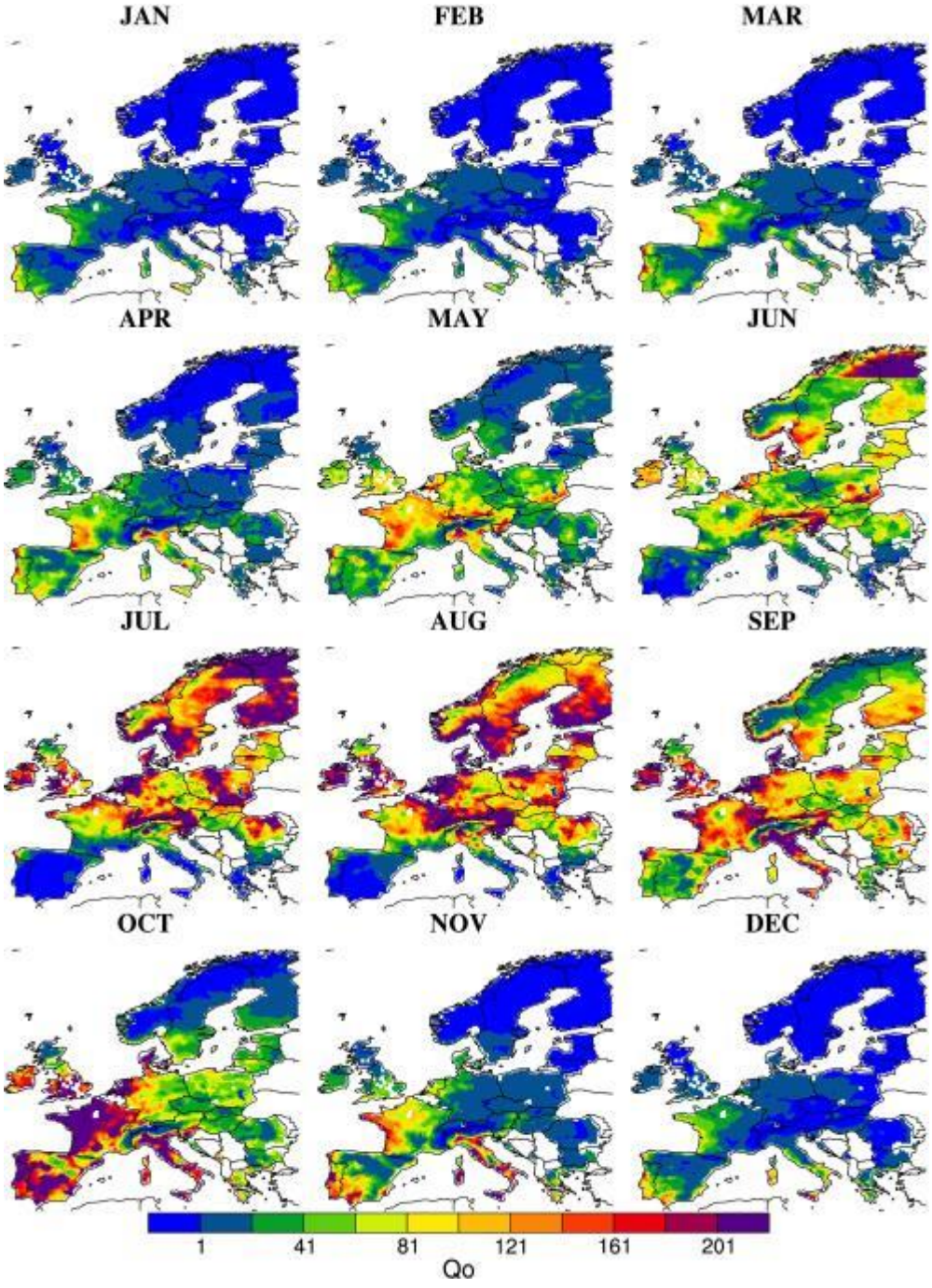

Fig. S5. Monthly estimates Q_0 based on the EOBS climate data for 1970-2013 and a constant sheep stocking density (H=1).

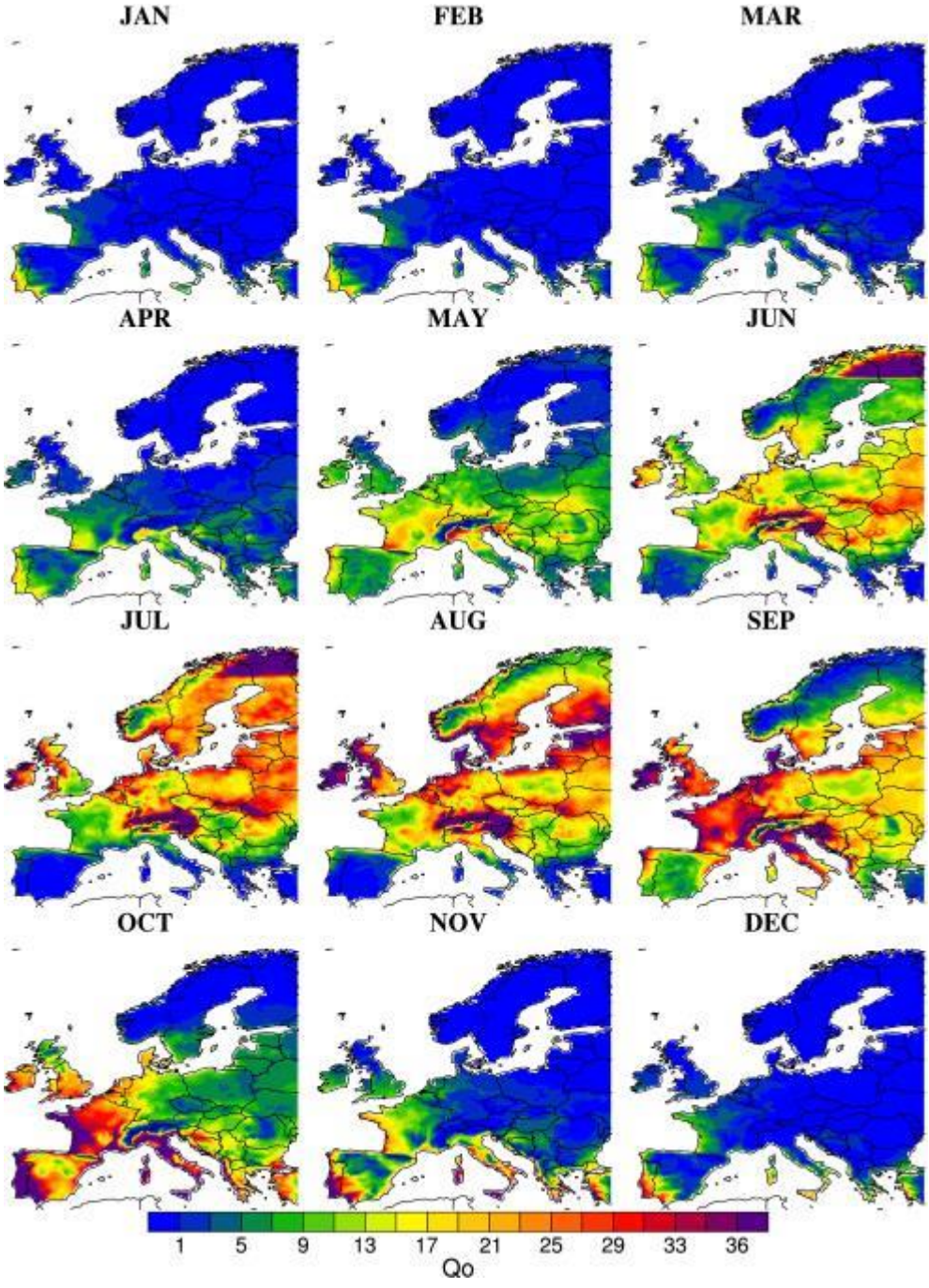

Fig. S6. Monthly Q_0 estimates based on the EOBS climate data for the 1970s (1970-1979) and a constant sheep stocking density (H=1).

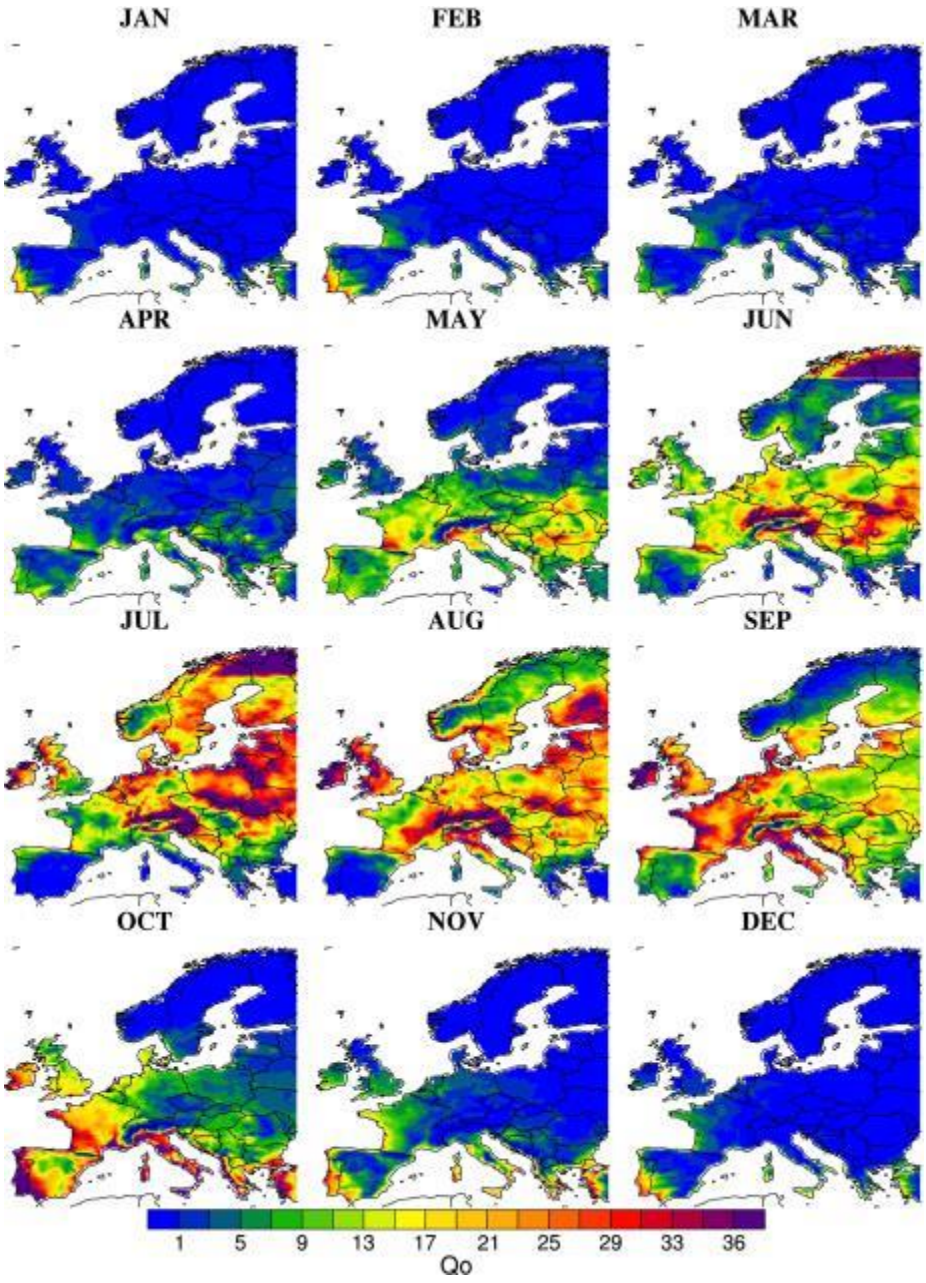

Fig. S7. Monthly Q_0 estimates based on the EOBS climate data for the 1980s (1980-1989) and a constant sheep stocking density (H=1).

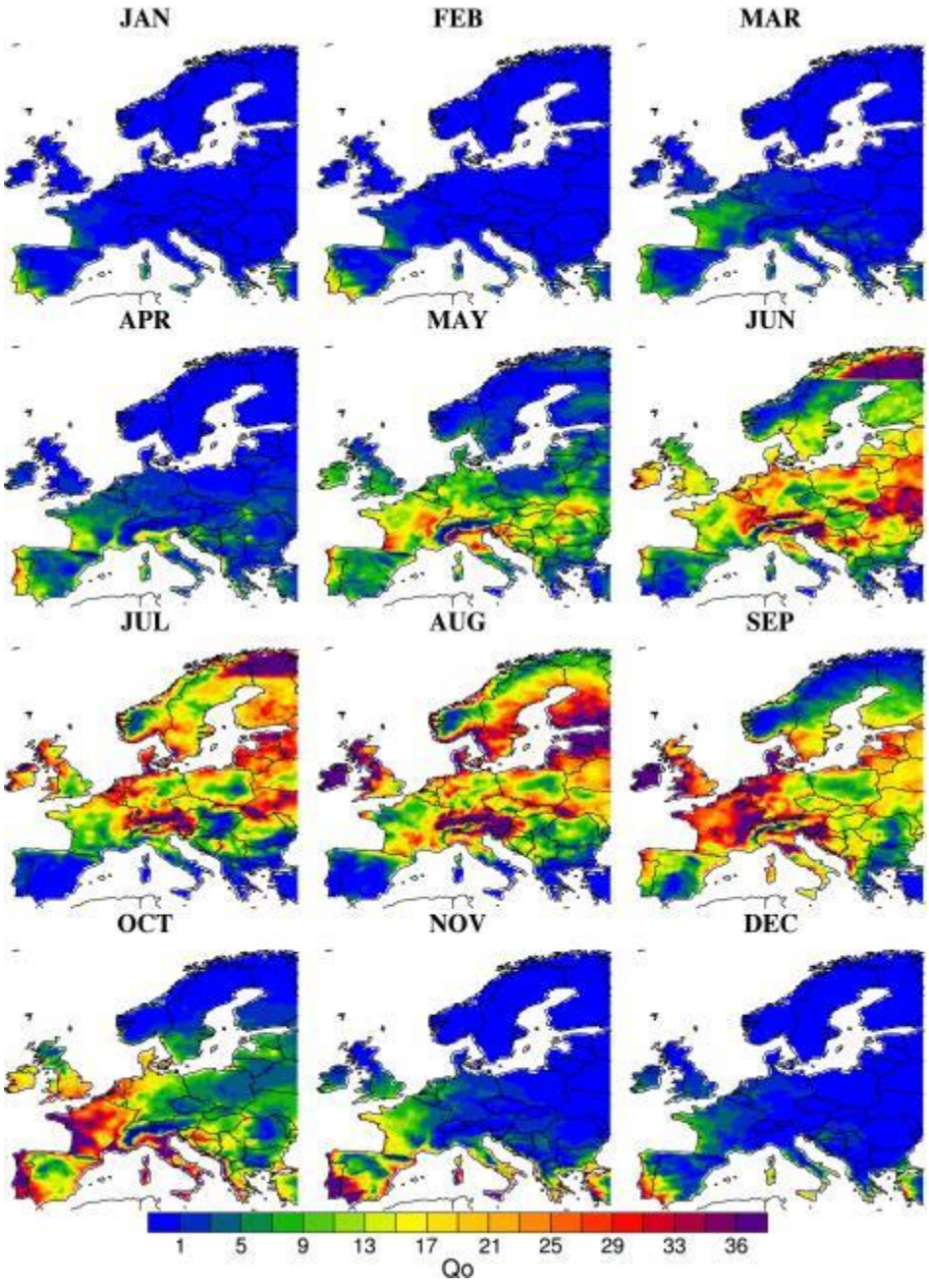

Fig. S8. Monthly Q_0 estimates based on the EOBS climate data for the 1990s (1990-1999) and a constant sheep stocking density (H=1).

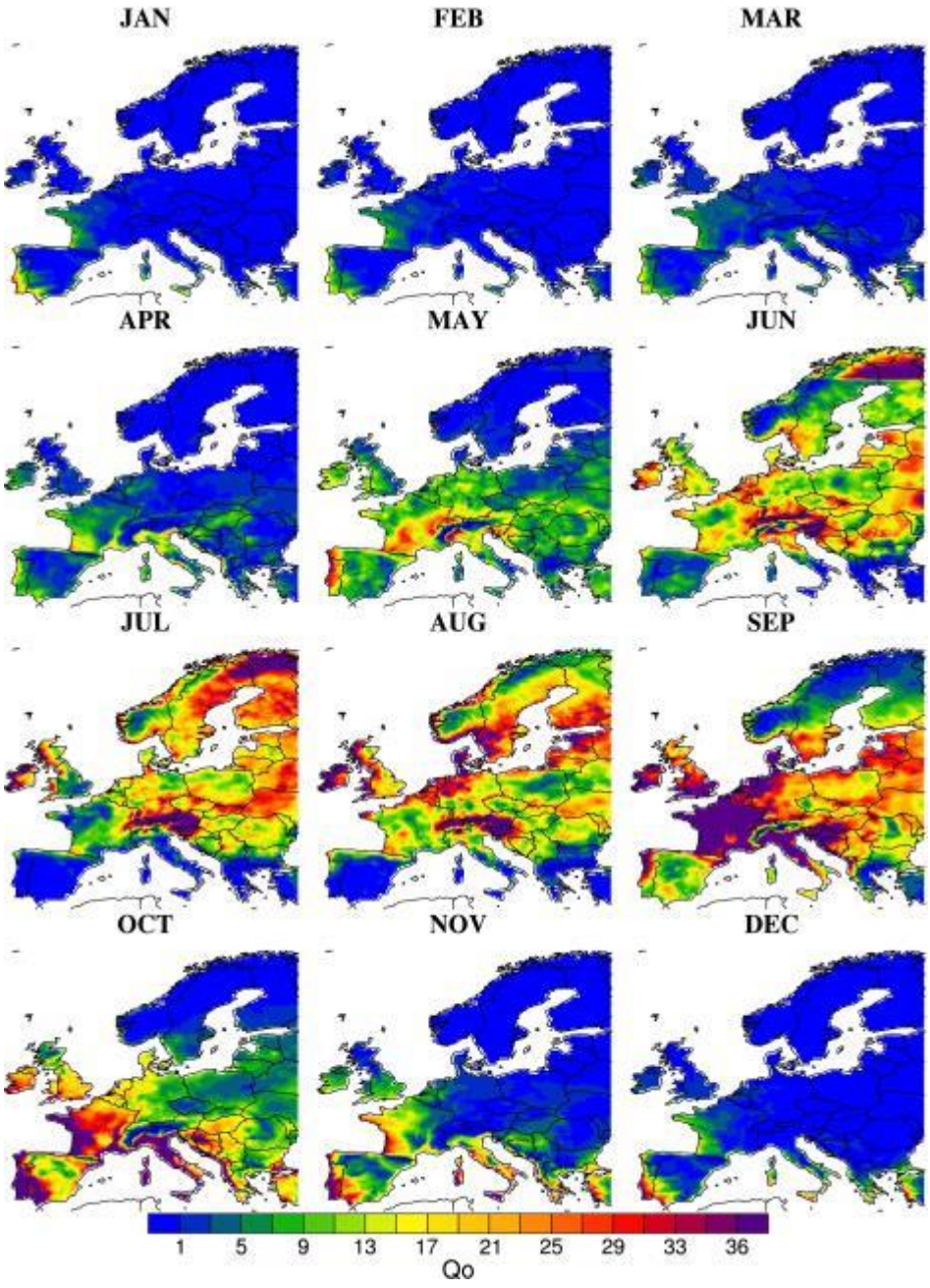

Fig. S9. Monthly Q_0 estimates based on the EOBS climate data for the 2000s (2000-2009) and a constant sheep stocking density (H=1).